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Inheritance of sugar and starch characters in corn

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(WITH PLATES 3–5)

The mass of the evidence accumulated in the last decade from the most widely varied material, both plant and animal, certainly indicates that judged by visible appearances for many cases at least the old question as to whether widely separated and heritably fixed types can be connected by finely graded intermediate forms has been settled in the affirmative. In view of the vast number of observations and experiments which have been made it is worth while not to lose sight of this positive result in the still existing conflict of rival theories. Such series of connecting links have been produced experimentally under rigidly controlled conditions by Castle, Jennings and others. It is still urged, however, that this apparent continuity of variation in visible characters is not a true index of what is occurring in the germ plasm. The old dogma of the fixity of specific types has been revived as a dogma of the fixity of the germ plasm. The units of the germ plasm, genes, factors, etc., it is urged, must be conceived as definite and unvarying except for special and rather cataclysmic alterations at relatively infrequent intervals.

The range of evidence as to continuity of variation covers all the common types of reproduction both sexual and asexual. To refer only to the most significant papers which have appeared we may note that such series of connecting links between widely diverse end products have been produced by Castle and Phillips

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('14) with hooded rats reproducing sexually and with inbreeding, by Jennings ('16) with *Difflugia* and by Hegner ('19) with *Arcella* reproducing asexually by simple cell division. Stout ('15) has also shown that such series can be produced by bud variation in *Coleus* and that by selection of these bud variants for specific leaf patterns races of purity and constancy sufficient for successful commercial uses can be produced. The facts as to the occurrence of widely divergent mutants or sports, which may or may not be monstrosities, and their fixity in heredity are in just about the same position as they were when Darwin concluded that such sporadic variations have probably not played any very significant rôle in evolution. The discovery that such forms as *Oenothera gigas* may have a tetraploid chromosome number is highly interesting and may indicate a possible method of effective evolutionary change, but the great mass of what have been more recently called mutants we are coming to realize are merely the extremes of series of fluctuating variants. There is adequate evidence, it seems to me, that such fluctuating changes may involve the fundamental constitution of the cells and may be expressed in chromosome changes as well as in gross characters. The discovery that forms may vary by a single chromosome is apparently established for *O. lata*. Kuwada ('11, '15 and '19) has claimed also, without however giving very adequate evidence, that the sugar corns vary in the number of their chromosomes from nine to twelve (haploid number) and that the sugar corns may have a larger number of chromosomes than the starchy corns. Such data are of great interest, but Kuwada's figures are not very convincing as he gives no full series of the stages for any one race. He lists nine varieties with which he worked. Four starchy races are reported as showing ten chromosomes (haploid number), one sugar corn as showing nine to ten and nine to twelve, respectively (haploid numbers). In his 1919 paper he attempts to utilize these observations in drawing conclusions as to the hybrid ancestry of corn.

As I pointed out ('12), in the recent genetical studies practically the first advance beyond the simple concepts that every visible character of a plant is due to, and transmitted by, a simple fixed factor which remains unchanged, except for certain rather rare and deep-seated changes resulting in mutations, was toward a theo-

retic provision for greater complexity in breeding results than these simple hypotheses allowed. Among Mendelians as well as others there is now coming to be rather general agreement that visible characters are due to several or even numerous more or less independently modifiable or varying units in the germ plasm. This change of viewpoint is due to the increasing number of cases which show more complicated results from crossing individuals differing in a single visible character than are provided for in the so-called monohybrid formula. The visible data in many such cases are a large number of individuals in the F_2 which do not show the character in question in sharply differentiated form, that is, the occurrence of intermediates as the older authors would have described them.

It has been universally shown by the actual data that in crossing sweet corns with flints in certain cases at least intermediate kernels appear in the F_2 which are not so plump as flints and not so wrinkled as a good quality of sugar kernels, but there has been a general tendency to disregard these facts in the interest of maintaining simple Mendelian expressions for the results of such crosses. Whether there are any races in which these intermediates do not appear is not altogether clear.

Sturtevant ('99) reports three varieties of what is apparently a similar intermediate type of corn, based on three ears sent him from the San Padro Indian collection of Dr. Palmer. He proposes the binomial *Zea amyleasaccharata*, "Starchy-sweet corn," for such types and states that he also obtained kernels of similar appearance from Peru in 1895. Sturtevant describes all these types as having the upper portion of the kernel sweet and the lower portion starchy, an interesting special case in the intergrading of these characters. Collins and Kempton ('13 and '14) believe that in the offspring of crosses between sweet and waxy varieties irregularities in the expected Mendelian ratios are due to a "failure of some sweet seeds to develop a wrinkled exterior." Correns ('01) made the investigation of the starch and sugar characters one of the main objects of his classic study of heredity in corn and has recorded his observations of the degree of wrinkling of the kernels in the F_1 and F_2 generations with considerable completeness. But Correns's conclusions and interpretations have

been more widely quoted than his actual data. He tested two sweet races, his No. III *R. caerulaeodulcis* and No. VI *R. dulcis*, both of which he describes as constant. The seed was obtained from Haage and Schmidt and both races are described by Koernicke ('85). The total number of crosses between sweets and flints and pops where only one kind of pollen was used was twenty-one. Eighteen were between flint and sweet races and two were between pop and sweet races. One involved the doubtful pop race *R. nana*. In five cases he reports as smooth or almost smooth the kernels in the F_1 from crosses of flints and sweets, but states without very detailed comparisons that the microscopic characters of these kernels are like those of thc starch-bearing parent.

In none of these cases are the reciprocals reported as showing intermediate kernels. In one case (p. 67 and *pl. 1, f. 50*) he figures a kernel which is markedly pitted or wrinkled at one point while the rest of the kernel is smooth and flint-like. In another case (p. 56) a sweet corn by a sweet corn gave some kernels not so deeply wrinkled as the parents, though he states, "the chemical composition of the endosperm was not changed."

In two cases (pp. 70 and 76) he reports a sweet (*R. caerulaeodulcis*) pollinated on the one hand by a pop corn (*R. leucoceras*) and on the other by a flint (*R. vulgata*) as giving some kernels slightly dent-like in type in the F_1. The first of these cases he figures in *pl. 1, f. 72*, and the second in *pl. 1, f. 87* and in *pl. 2, f. 77*. In the latter case an entire ear is shown with most of the kernels slightly dimpled and a few with quite characteristic but poorly developed wrinkling. Correns also (p. 88) notes a tendency in crosses of sugar corn by flint types to what he regards as approaching a dent form of kernel in the F_1. He also notes (p. 89) that in crosses of flints by sweet types occasional kernels show an approach to the sweet type in the F_1. Correns found in his pure sweet race (*R. dulcis*) occasional kernels which are less wrinkled or almost smooth (pp. 39 and 40, *f. 4c, 5b*, and *pl. 1, f. 22*) and explains them as having a larger air cavity and a larger mealy area making this a general explanation for intermediates (p. 39).

His figure of a section of such a kernel (p. 38) does not make clear that there is a larger air cavity in such grains but his figure (*pl. 1, f. 22*) gives a fairly good representation of the appearance of such

kernels as I have found them. Both these figures are from kernels of his pure race (*R. dulcis*). Correns does not give figures of any of his F_1 kernels, which he describes as "almost smooth," but apparently regards them as like those figured from the pure race. He describes the F_2 generations from only three of his sweet flint and pop crosses making the general statement that those described are typical of the whole series. In the first of these three, Exp. 107, (*R. rubra* × R. *dulcis*) × *R. dulcis* (back cross by recessive on F_1), out of 140 kernels he obtained 50 per cent wrinkled kernels, 5.8 per cent intermediate kernels, 44.3 per cent smooth kernels, the F_1 generation having given only smooth kernels.

The F_3 generation, Exp. 108, (*R. rubra* × *R. dulcis*) × *R. dulcis*, in which the wrinkled kernels of the F_2 were grown and pollinated by the original sugar parent (back cross on extracted recessive) gave three ears, two of which were all wrinkled, but in the third about one seventh of the kernels were "only slightly wrinkled." The parallel F_3 generation, Exp. 109, in which the smooth kernels of the F_2 were grown and pollinated by the original *R. dulcis* gave one large and two poor ears on one plant. Correns reports the kernels as "about half smooth and half wrinkled, some only slightly." He reports counting only part of the kernels, of which 82 were wrinkled and 2 almost smooth, 74 smooth; that is "53.2 per cent more or less wrinkled and 46.8 per cent smooth," the expectation being of course 50 per cent wrinkled and 50 per cent smooth.

Correns's Exp. 110 is identical with Exp. 108, so far as the characters sugar and starch are concerned. He considers this experiment open to question since of two plants, one gave three ears all wrinkled, the other gave one medium-sized and one small ear in which half the kernels were smooth and half were wrinkled "rather many only finely wrinkled or almost smooth" but otherwise the endosperm of typical sugar consistency. Whether or not these results are due to an error in records or manipulation there is no question that here again the intermediate sweet starch kernels appeared whatever their parentage may have been.

Exp. 111 again duplicates Exp. 109 so far as the characters sweet and flint are concerned. In the case of two individuals the proportions were 50.1 per cent smooth, 49.9 per cent wrinkled,

expectation 1:1, but from the third plant very many of the kernels were very slightly wrinkled though translucent like typical sweet kernels.

In the F_2 of his cross, *R. dulcis* sweet × *R. vulgata* flint, Exp. 112, in which four plants were allowed to pollinate freely among themselves, Correns reports that because of too late planting the ears for the most part did not become entirely ripe.

In Exp. 113, (*R. vulgata* flint × *R. caerulaeodulcis* sweet) × *R. dulcis*, which is a back cross of the recessive parent on the F_1 hybrid, he mentions that some kernels which were classified as sweet were almost smooth but their transparency indicated that they belonged with the sweet type. For Exps. 114, 115, 118, 119, 120, 121, 126, 127, no mention is made of kernels intermediate between sweet and flint.

SUMMARY OF CORRENS'S F_2 AND LATER GENERATIONS

107. 58 per cent of all kernels intermediate.
108. 1 ear of 3, one seventh of kernels only slightly wrinkled.
109. Some only slightly wrinkled.
110. Doubtful experiment, but in one ear rather many kernels only minutely wrinkled or almost smooth.
111. One plant of three gave many kernels, slightly wrinkled though translucent.
112. No intermediates mentioned.
113. Some kernels classed as sweet were almost smooth.
114, 115, 118, 119, 120, 121, 126, and 127. No mention is made of intermediates.
Fifteen experiments gave no intermediates.
Seven experiments gave intermediates.

The above summary of Correns's results on the F_2 and later generations from crosses between sugar and starch races shows that in seven out of fifteen experiments reported in which sweet kernels were expected some kernels of intermediate form appeared, in one case 5.8 per cent of the total number of kernels were intermediates. Correns in no way attempts to conceal this result but treats it as unimportant. He regards these kernels as sweet in type but with a larger air cavity and more mealy (p. 39). He seems not, however, to have selected these aberrant kernels and planted them, which of course, as he so frequently emphasizes, is the only proper test of the significance of such characteristics.

Correns in 1902 reports further on starch and sugar crosses. In an extensive test of the Mendelian formula he obtained 10,372

smooth kernels, 3,388 wrinkled kernels and 12 somewhat wrinkled. He includes the latter with the smooth instead of as above with the wrinkled, giving 75.4 per cent smooth, 24.6 per cent wrinkled. Again he does not report the behavior of the partly wrinkled kernels when grown. He also further tested the ratios obtained in a cross between Black Mexican sweet and Rice Pop Corn var. *leucoceras*, and found in the selfed F_2 generation an excess of smooth kernels. Instead of 75 per cent smooth and 25 per cent wrinkled he obtained in an extensive series 84.5 per cent smooth, 15.6 per cent wrinkled. In another extensive series 81.9 per cent smooth and 18 per cent wrinkled, no intermediates, are reported. Correns concludes these results are to be explained not on an assumption of segregation in some other than a 1:1 ratio but as due to partial failure of certain combinations to develop, or to selective or differential pairing. In the presence of a great excess of pollen on the silk certain grains might well take precedence by reason of their greater vigor in the particular combination possible to them. I am discussing these sweet $\times$ pop crosses in another paper.

As figured by Correns and as I find them, certain sharply pitted (*pl. 1, f. 50*) and chimaera-like (p. 39) kernels of the F_1 are quite different in appearance from the intermediately wrinkled kernels noted above. Correns does not test the behavior of these pitted and half and half kernels when grown and selfed. It is not impossible that they owe their appearance to special interactions of the germ plasms in the triple endosperm fusion and subsequent divisions and are not an index of what has happened in the fusion of the egg and male nuclei and the development of the embryo. I shall report elsewhere on the behavior of certain of these kernels when grown and selfed.

Correns, while making corn the type of his third class of the possible combinations of dominance and segregation (homodynamic schizogonic) in which the F_1 is more or less intermediate between the parents so that dominants, hybrids, and recessives are visibly different, does so on the grounds of the behavior of aleurone and endosperm colors, etc., and claims that the starch-sugar pair are heterodynamic with dominance of the starch character in the F_1 and later hybrids, (pp. 67, 86, 141).

East and Hayes ('11, pp. 33–34) had some four hundred hand

pollinated F_2's from crosses between sweet and flint, but report in detail on only one fourth of them, the remainder showing as they say "nothing different." They (p. 34) state that in the F_1 dominance is apparently complete. "In no case was there the slightest difference between the homozygous and the heterozygous seeds either in outward appearance or in the character of the starch cells when examined microscopically" though they note the occasional occurrence of the curious chimaera kernels with one side smooth, the other side wrinkled, which were also observed by Correns and others. They further concluded that the characters starchy and sweet are the same in all races so that all crosses behave alike. They had not of course tested at this time the crosses between waxy and sweet, later described by Collins.

East and Hayes report, however, that ears intermediate between sweet and flint do appear in various races of sweet corn and may give trouble to canneries since they transmit the character. They state that such ears appear in ratios not to exceed one in 10,000, but do not give the detailed statistical data on which the numbers are based. They also report one case in which three semi starch ears appeared in the progeny of an extracted recessive from a cross of Illinois High Protein Dent by Black Mexican Sweet. The entire ear was "rather uniformly semi starchy." The offspring of its more starchy kernels varied from as starchy as the parent to more starchy. Those from the less starchy kernels were in part good sweet kernels and in part semi starchy. Seeds could be selected which formed a series running from true sweet to true starchy. They reject the idea of impure segregation as accounting for such observations and hold that "dominant starchiness—if it is the same dominant starchiness—has been formed anew." They recognize also that certain races of sweet corn (Crosby) tend to have plumper kernels than others. Still in spite of all this they persist in regarding the factors for sweet and starchy as fixed and recognizably distinguishable categories. In a footnote (pp. 40–44) they argue the possibility that when pop corns are pollinated by sweet corns the smaller size of the kernels on intermediate ears may lead to their being more nearly filled by the endosperm materials and hence less wrinkled in appearance, they do not however give any further data on this

point from their own work. East and Hayes believe (p. 42) that these intermediates are not an evidence of the mixing of the sweet and starch characters but are due to progressive variations constantly taking place in small number along paths that have been passed before, and assert like Correns the dominance of the starch character over the sweet character, regarding the behavior of the two characters as an example of a simple Mendelian monohybrid.

I have reviewed the work of Correns and East in some detail on this point to show that from the first the ocurrence of such intermediates constituting exceptions to the simple formula for a Mendelian monohybrid were observed though they were regarded as unimportant from the theoretic standpoint. In spite of these observed cases of intermediates the combination of sweet with starch corns is made a standard type to illustrate Mendelian behavior in such summaries and general discussions as Correns's "Die neuen Vererbungs-Gesetze" ('12); Baur's "Einführung in die experimentelle Vererbungslehre," 2d edition ('14); Haecker's "Allgemeine Vererbungslehre" ('11); and even the new manual, "Genetics in Relation to Agriculture," by Babcock and Claussen ('18).

It is highly desirable, it seems to me, to know whether in attempting to maintain sweet races at their highest perfection and in breeding for new varieties it is necessary to exclude these intermediates in selecting seed. East and Hayes, as noted, make the general statement that as rather rare mutants they may cause considerable trouble to canners but without referring to specific instances.

Jones ('19) reports the continuance of a selection experiment with the three intermediate ears obtained by East and Hayes, and referred to above. The aim of the experiment was to recover, if possible, the parent starchy and sweet types by selecting from the selfed offspring of this intermediate. Beginning in 1907 the selection for starchy was carried through ten generations and that for sweet through nine generations. Jones obtained in this way a sweet race whose kernels still vary somewhat in the amount of opaque substance which they contain, though in general they are good sugar types and what he calls a pseudo-starchy race, in which the kernels are in some ears perfectly plump while in others there

may be areas on a few seeds which closely resemble the wrinkled condition of sweet seeds. In general it is stated this pseudo-starchy race when crossed with pure starchy races gives in the F_2 segregation into sugary and starchy kernels as if it had been a so-called pure sweet though the F_2 kernels so obtained show considerable tendency to pseudo-starchiness in later generations in a fashion that makes the results hard to classify. The explanation of his observations, Jones believes, is to be sought in the recognition that more factors are concerned in the determination of the sweet and starch pair of characters than had before been realized.

He makes no claim to have reached an adequate or theoretically satisfying analysis from the Mendelian standpoint. His assumed three factors are merely taken "as an illustration" and he speaks of the "indefinite nature of the character."

Jones refers (p. 388) to other cases he has observed in which intermediate kernels have appeared in starch and sugar corn crosses, though he expresses no opinion as to the frequency of their occurrence, and leaves the question of their nature and origin much as it was before. He recognizes the possible influence of the fact that the mother plant is always one generation in advance of the endosperm, though a real test of the significance of this situation is difficult to achieve.

On the assumption of relatively fixed unit factors, it is rather striking when this intermediate condition has appeared that new and definite combinations of the factors assumed are so difficult to achieve. Neither the pseudo starchy nor the segregated sweet, either in appearance or behavior, when bred seem quite to meet the standards of a homozygous race in the strict sense of Johannsen. We seem to have here the familiar phenomenon which was known to the older breeders as "breaking up" of types in the second and following generations as a result of hybridizing. From the standpoint of current theories we are inclined to focus our attention upon the possibility of recovering parent types after hybridizing while the older breeders regarded this phenomenon, though familiar, as of little interest compared with the cases in which "breaking up" occurred. The search was frequently so far as hybridization was used in breeding for practical ends for a cross in which breaking up would occur. A species with desirable basic

qualities of color, form, habit of growth, etc., was tested in various combinations until one was found which would give a series of variants of these basic qualities, such as we find in so many groups of cultivated plants.

It is to be hoped that Jones's experiments can be continued till an adequate unit factorial analysis for corn is, if possible, attained. The economic importance of the crop will certainly justify this procedure. Judging his data as they stand, however, it seems to me that the assumption of fluctuating variations and mutual modification of the germ plasms with each succeeding sexual reproductive cycle of synapsis, chromosome reduction, cell and nuclear fusion and chromosome pairing fits the facts much better than that of numerous fixed unit factors merely shifting their interrelations through the almost endless number of the mathematically possible combinations which, it is assumed again, they can enter with equal freedom.

My results agree with those of Jones that these intermediate kernels tend rather strongly to propagate their kind and that races with a strong tendency to their production can be isolated by selection. I am discussing elsewhere the possible importance of such races as what I have proposed to call meal corns. If corn is to be used increasingly as a food more attention should be paid by breeders to improving the flavor and general palatability of corns to be used in making meals.

In my own work intermediates have appeared in practically all of my crosses between sweets and flints, dents, flour corns, and pop corns. I have also observed cases of the spontaneous appearance of intermediate kernels in the pure bred Black Mexican Sweet and some other sugar corns which I have used. Such intermediate kernels in so-called pure races occur scatteringly on occasional ears and I have observed one ear which showed a general tendency to this condition. This ear probably came from an accidentally planted intermediate kernel. As noted above Correns does not report on any attempts to learn how the hybrid F_1 and F_2 kernels which he reports as "slightly wrinkled" or almost smooth would behave when grown and selfed or crossed back on their sweet or starch parents. The occurrence of such intermediates arising by all the various methods noted is of particular interest in view of the

tendency to overlook such fluctuating differences in the interest of attempts at broad generalizations.

I have endeavored to settle the points here involved and have grown a number of such intermediates which have appeared in various crosses between sweets, and flints, dents and pops.

The study of these endosperm characters is of special interest since the endosperm nuclei in general are the product of a triple nuclear fusion; in each case two nuclei from the mother combine with one from the male parent. The effect of this unequal representation of the two parents in the endosperm can be checked up by comparison with the expression of the same characters as transmitted to the next generation through the embryo which arises from the normally fertilized egg. The morphological nature and phylogenetic origin of the triple fusion in forming the primary endosperm nucleus have not been as yet worked out, but functionally and from the genetic standpoint it is a triploid growth which is crowded out and absorbed by the normal embryo. The study of reciprocal crosses with reference to the expression of these endosperm characters afford ideal conditions for determining the effects of a double as contrasted with a single set of chromosomes from the same parent, so-called dosage phenomena, etc. I shall not take up these questions in the present paper since I desire first to establish and clear up the facts as to the occurrence of intermediates between starch and sugar corns and the behavior of these intermediates when grown and selfed.

The interesting paper by Weatherwax ('19) establishes the fact that the embryo sac in corn is formed after the manner of the dicotyledonous rather than the lily type so that there is no possibility that either of the polar nuclei which fuse in the endosperm nucleus or their parents were formed by a reduction division and the possible complications as to the so-called genetic constitution of the nuclei of an endosperm of the lily type are not present in corn.

I have worked with the following races:

Four flints: Canadian Early Yellow, Longfellow, Long White Flint, and Hall's Golden Nugget.

Eight dent corns: Wisconsin White Dent, Silver King, Bloody Butcher, Gaunt's Golden Dent, Long's Champion Dent, King Philip Red Cob, Eureka Dent.

Six sugar corns: Crosby's Early, Country Gentleman, Ruby Sweet, Golden Bantam Sweet, Golden Cream Sweet, and Stowell's Evergreen.

Five flour corns: Red Squaw, Blue Flour (Pink Flour, Yellow Flour, and White Flour from Arikara Indians).

Six pop corns: Eight Rowed Pop, White Rice, Black Beauty Pop, Snowflake, Golden Tom Thumb, and California Golden.

With the exception of the corns from the Arikara Indians, these are all fairly common and well marked races which I have grown in selfed or inbred cultures parallel to my experiments with crossing and have found to come true to type except for such fluctuating variations as I am noting in connection with the experiments. That such fluctuating variations occur in both sexually and asexually reproduced series, is well established as noted, but that sexual reproduction favors their occurrence is, it seems to me, shown especially well by the results obtained in breeding corn.

My results can best be presented perhaps by reproducing life-size photographs of a series of ears (PLATES 1–3) illustrating the actual number, distribution, appearance, etc., of these intermediates from a characteristic generation in a series of experiments which I have carried on now for some six years. These figures can be regarded as typical of the fuller series reported statistically in the tables, which show the proportions of the various classes of kernels in the successive generations. They represent a stage in which the injurious effects of selfing are not yet seriously manifest. They are also illustrative of my results in all the sweet with flint or dent combinations noted below, with many of which I have worked for some six or seven years. I am reporting also on sweet with pop corn crosses and some further special cases in another paper.

PLATES 1–3, FIGS. 130 *a*–130 *f*, illustrate the F_3 of a cross between a large white dent obtained from Thorburn as Wisconsin White Dent, and the common Black Mexican sweet corn, also obtained from Thorburn. I am not reproducing figures of these two parent races since the types are well known and, though both ears are undersized and not well filled at the tip, due in part to selfing, FIG. 130 *a* for the sweet type and FIG. 130 *f* in its dent kernels for the starchy type may be taken as illustrating the kernel characters of the parents of the series. The kernels of Wisconsin

White Dent do not always show the pronouncedly wrinkled tip typically seen in dents. The kernels frequently show only a smooth transverse groove and the horny endosperm comes nearer the tip, leaving less of the opaque white endosperm. These kernels with less wrinkled tips have been called dimpled dents. They are well shown in the FIG. 130 *f* and as noted the dent kernels of this ear represent the dimpled dent kernels of the original starchy parent. They occur in the inbred ears but become much more numerous in the crosses with sweets. As in most dents the kernels at the butt and tip of the ear tend to pass over into the dimpled form or even to be quite smooth and flint-like, though generally showing more or less opaque endosperm.

I have not employed field tests on a large scale in my studies but have endeavored to use all the precautions for careful control in pollination with relatively small numbers of plants. I have used both the method of bagging the ears and tassels separately and transferring the pollen by hand, and the method of connecting tassel and ear by a paper tube and allowing the pollen to reach the silk directly. In spite of the fact that only one crop per year can be obtained, the large numbers of kernels on an ear, all produced under quite similar conditions, and the possibility of checking up results year after year on the preserved material in a fashion quite impossible with flower colors, etc., make corn a favorable material for such studies on the variation of characters, etc.

As noted above, there is general agreement as to the occurrence of intermediates between sugary and starchy kernels. I shall report particularly the numbers in which these intermediate kernels occur in the successive generations and their behavior when grown and selfed.

I have carried the cross between Wisconsin White Dent and Black Mexican Sweet, both obtained from Thorburn, through four generations, from 1912–1916 and will give my results with this series in some detail as noted, since they are illustrative of all my results in crossing sweet and flint or dent types. The tassels and ears were bagged separately for the most part though in some cases they were connected directly by paper tubes.

Three ears, 5 *a*, 5 *b*, and 5 *c*, were obtained in 1912 by pollinating the Wisconsin White Dent with pollen from the Black

Mexican Sweet and showed no intermediate kernels. They varied from a wrinkled to a dimpled or rather flint like dent, but showed no evidence of xenia so far as the starch sweet characters are concerned; the color inheritance I shall discuss elsewhere.

I obtained thirteen selfed ears of the F_2 generation (Nos. 129 *a–f*, six ears, and 130 *a–g*, seven ears) in 1913. In these ears the intermediate kernels when only superficially examined can be confused sometimes with the dents which also show wrinkling, though only at the tip. The translucency and general shrinkage of the sweet kernels when fully developed are however unmistakable, as are also the opaque white and shrunken tips of the dent. Some of the intermediates shade over into the sweet type and others toward the dent type. Those half way between sweet and dent can be recognized with certainty but others may be doubtful.

TABLE I. SELFED F_2 EARS OF CROSS WISCONSIN WHITE DENT × BLACK MEXICAN SWEET

Ear Nos.	Starchy	Intermediate	Sweet
129 *a*............	277	5	96
" *b*............	215	0	64
" *c*............	315	3	119
" *d*............	204	5	76
" *e*............	329	5	133
" *f*............	91	5	22
130 *a*............	297	4	104
" *b*............	154	4	43
" *c*............	138	2	41
" *d*............	239	13	63
" *f*............	279	21	84
" *g*............	345	6	124
	2,883	73	969

The classification of the kernels from these thirteen ears is given in TABLE I, which shows in the totals 2,883 starchy kernels to 969 sweet kernels, and 73 apparently intermediate kernels. This is a ratio of about 73.45 per cent starchy: 1.85 per cent intermediate: 24.68 per cent sweet. If we class the intermediates with the starchy kernels we have a ratio per four of 3.01 starchy: .98 sweet. If we divide the intermediates equally between the starchy and the sweet kernels we have a ratio per four of 2.97 starchy: 1.02 sweet. If we class the intermediates with the sweets,

as Correns has done we have a ratio per four of 2.93 starchy: 1.06 sweet. The divergence from the Mendelian ratio is least when the intermediates are classed with the starchy kernels though the basis of their selection was that they were somewhat wrinkled. As noted above we can also distinguish here an intermediate in the starchy kernels between dent and flint. In these so-called dimpled dent kernels the opaque whiteness and large wrinkled depression of the tip of the dent kernel is much reduced. They shade over into typical dents on the one hand and typical flints on the other, and the classification is not always easy to make. I have not attempted to separate them here but have done so in connection with the ears photographed from later generations.

Kernels from four of these F_2 ears, 129 *a*, 129 *c*, 130 *a*, and 130*d*, were grown and selfed in the next (F_3) generation (1914). The kernels were selected with reference both to the inheritance of the sweet and starchy characters and the aleurone color. I shall consider here only the results with the sweet and starchy characters leaving the data as to the inheritance of aleurone color for a later report. I will take up first the results obtained from selected intermediate kernels.

Ear 130 *d*, showing a fair number of intermediate kernels, was selected as the parent for the next generation of intermediates. The thirteen white intermediate kernels were planted and six ears were obtained from this lot in 1914, which ranged from one (164 *a*) which had almost all its kernels typical sweets to another (164 *f*) which had a large proportion of dimpled dent and more typical dent kernels, though the photograph is hardly adequate to distinguish the latter from the dimpled type, especially in the rows in which the kernels are seen directly in end view. I have taken this F_3 series as illustrating as fully as possible the facts regarding these intermediates and have had them photographed and reproduced life size so that the degree and character of the fluctuations can be studied as they appear in the originals. This seemed preferable to giving a larger number of less perfect illustrations. The series is shown in the photographs and the classification of the kernels is given in TABLE II, section 1, *A*. A dark intermediate kernel from the same ear (130 *d*) gave an ear of all sweet kernels (167 *a*) like 164 *a* of the white series and is included

in the table though not figured, as it shows nothing further than is shown by 164 *a*.

TABLE II. CROSS WISCONSIN WHITE DENT × BLACK MEXICAN SWEET
1. F_3 EARS FROM SELFED F_2 EAR 130 *d*, 1914
A. Selected intermediate kernels planted

Ear Nos.	Dent	Dimpled Dent	Flint	Interm.	Sweet
164 *a*.......	0	0	0	8	163
" *b*.......	0	0	0	133	71
" *c*.......	0	3	0	132	52
" *d*.......	0	0	0	123	62
" *e*.......	0	12	0	177	56
" *f*.......	32	86	40	43	35
167 *a*.......	0	0	0	0	309
	32	101	40	616	748

The pure starchy kernels as noted vary from flints which are quite smooth and more or less translucent and horny to dimpled dents in which there is a slight groove at the tip. From this dimpled dent form they range further toward more typical dents with wrinkled as well as grooved tips and with a well marked opaque white color due to intercellular air spaces.

Ear 167*a* is a pure sweet showing no marked intermediates, as noted; ear 164*a* is almost pure sweet, showing eight intermediate to 163 sweet kernels, a ratio of about 4 per cent intermediates to 95 per cent sweet. The intermediates here also incline toward the sweet type in amount of wrinkling and translucency, though easily distinguishable from the typical sweet kernels.

As the photograph shows, ear 164 *f*, also from an intermediate kernel is in general quite of the dimpled type, but with conspicuous sweet and intermediate kernels scattered among the dent-like kernels. The classes here are 158 starchy to 43 intermediate and 35 sweet. If we divide the intermediates equally between the starchy and the sweet classes, we shall have 179.5 starchy to 56.5 sweet, or 3.042 starchy to .957 sweet, a good Mendelian hybrid ratio. But if as Correns did, we add the intermediates to the sweet class, we get 2.67 starchy to 1.32 sweets. The extremes of the six ears range then from one almost pure recessive ear to one more like a so-called hybrid ear as they have been perhaps sometimes classed. It is not impossible that if larger numbers had

been planted, an ear approximating a pure dominant would have been obtained. The results become clearer from a consideration of the remaining four ears from these intermediate kernels. It is obvious at once, however, that the range of variation in the characters sweet and starch in these F_3 intermediate kernels extends in some cases at least so as to include both of the original parent types. There is no evidence in this case of the segregation at once of a factor or group of factors for intermediate nor of the production of a mutant which then at once breeds true.

The other four ears of the series, ears 164 *b*, *c*, *d*, and *e*, bring out still more clearly the fluctuating character of the qualities here involved. Ear 164 *b* gives only sweet and intermediate kernels, 133 intermediate to 71 sweet, a ratio of 34 per cent sweet to 65 per cent intermediate. The translucency of most of the kernels gives the ear the general appearance of the sweet type but the opaque white of the intermediate kernels is also conspicuous and their less wrinkled surfaces make them easily recognizable in the photograph.

Ear 164 *c* shows three dimpled dent kernels with 132 intermediate and 52 sweet, a ratio of about 1+ per cent starchy: 70+ per cent intermediate: 27+ per cent sweet. The number of intermediates is larger here again than the number of sweet kernels, and three dimpled kernels appear.

Ear 164 *d* should probably be classed as giving only sweet and intermediate kernels though it is difficult to be certain of the character of the kernels at the ends of two of the rows and two kernels should perhaps be classed as flints. Counting them as intermediates we have 123 intermediates to 62 sweets, something like a ratio of 2:1. The position of this ear in such a series as we have here is perhaps doubtful. It has a larger proportion of fully wrinkled kernels than ear 164 *c*, but on the other hand its intermediates tend more toward the dent type, especially in color. The ear in general shows more opaque white than ear 164 *c*, in which the translucency due to the sweet character is more in evidence.

Ear 164 *e* gives 12 dimpled dent kernels, some of which are almost flint-like; 177 intermediate and 56 sweet, a ratio of 4+ per cent starchy: 72+ per cent intermediate: 22 per cent sweet.

The proportion of pure sweets to intermediates is somewhat reduced. If we here class the intermediates with the starchy kernels we should have a ratio per four of 3.08 starchy and intermediates to .91 sweet.

The translucency of the intermediates is much less in this ear than in ear 164 *c*. The kernels tend also to be less wrinkled and as the photograph shows the ear has a greater resemblance to the parental dent type than the figures in the table indicate.

These four ears 164 *b*, *c*, *d*, and *e*, show in general two intermediates to one sweet kernel and it would be quite possible to conceive of a Mendelian factorial hypothesis to fit their case. Taking the whole series the facts suggest rather that in selecting intermediates one is inclined to select kernels of pronouncedly intermediate character and pass by those which are doubtful, leaving them in the sweet and starchy classes. Allowing for this tendency in selecting there would none the less seem to be evidence that intermediates tend rather to vary toward the sweet character than toward the starchy character. All six ears show large proportions of typical sweet kernels while only three of them show typical starchy kernels.

It is obvious that there is a marked tendency to the perpetuation of the intermediate condition when once it has appeared. Still it can by no means be maintained that intermediate kernels at once breed true. As shown in the table two ears (164 *a* and 167 *a*) from kernels selected as intermediates appear to be almost typically sweet, and one ear (164 *f*) has a high percentage of typically starchy kernels; 66+ per cent of starchy kernels, 18+ per cent of intermediates and 14+ per cent of typical sweet kernels. The remaining four ears vary in their proportions of intermediate kernels, to sweet kernels, neglecting the starchy kernels, from, roughly, 2:1 to 3:1.

This fluctuation in the occurrence of intermediates is still further illustrated in the offspring of six further lots of kernels selected from this same F_2 ear (130 *d*) to test the behavior of what appear to be pure sweet and pure starchy kernels, respectively. These lots were selected with reference to endosperm color as well but we shall consider only the sweet starch characters here. Four of the lots (Nos. 160–163 inclusive) were typical dimpled

dents and two lots consisted of typical sweet kernels (Nos. 165, 166). The dimpled dent lots were selected to represent colors from dark or blackish to white but we may treat them as one series with reference to the starch sweet characters. Twenty-four ears and nubbins were obtained from these dimpled dent starchy kernels (Nos. 160–163) of which twelve showed few intermediates and almost all dent, dimpled dent, and flint like kernels (extracted dominants) and twelve showed conspicuously dent, dimpled dent, flint, intermediate, and sweet kernels (F_3 hybrids).

TABLE II (*con.*)

B. Selected dimpled dent kernels planted

a. Mixed ears (hybrids) obtained

Ear Nos.	Starchy.	Intermediate.	Sweet.
160 *b*–1	147	35	13
" *b*–2	183	26	17
" *d*	17		9
" *f*	27	10	3
" *g*	129	14	37
" *h*–1	159		56
" *h*–2	33	3	58
161 *a*	126	13	47
162 *a*	89	5	34
" *b*	142		43
" *m*	179	43	1
163 *d*	159	5	51
	1,390	154	369

The proportion of intermediates in all these ears as will be seen is much smaller than in the case of the offspring of the F_2 kernels selected as intermediates. The ears of this class of F_3 hybrids as shown in TABLE II, section 1, *B*, *a*, give 1390 starchy to 154 intermediates to 369 sweet kernels, that is 2.9 starchy to .32 intermediate to .76 sweet. There are here in addition to the kernels which are plainly intermediate some others which approximate starchy kernels on the one hand and sweet kernels on the other. The classification is difficult in some cases since there is really a series from starchy to sweet. I have put in the class of intermediates only those that were plainly from their form and degree of translucency neither typical starchy nor typical sweet kernels. Here as in other cases it would be possible to make more than one class of intermediates but the lines of distinction would

be vague. If we should make but two classes putting all kernels that show any trace of wrinkling together we should have 1,390 starchy kernels to 523 more or less wrinkled and translucent kernels, a proportion per four kernels of 2.90 : 1.09. If we should divide the intermediate group equally between the starchy and sweet classes we should have more nearly an exact Mendelian ratio, 1,467 starchy to 446 sweet, that is 3.06 starchy to .93 sweet, as noted. Correns as noted treated the "slightly wrinkled" and "almost smooth" kernels he observed as sweet kernels.

The twelve ears which showed no typical sweet kernels gave a very low proportion of intermediates. Seven of these ears give no intermediates. The other five ears give only from one to four intermediate kernels, the total being 2,397 starchy to 11 intermediate kernels, 267 starchy to 1 intermediate. The classification is difficult here also and I have included only kernels of undoubtedly intermediate appearance in that class. The numbers of kernels of the different classes for these ears are given in TABLE II, section 1, *B*, *b*. As noted they are the so-called extracted dominants.

TABLE II (*con.*)

b. Slightly mixed ears (dominants) obtained

Ear Nos.	Starchy	Intermediate	Sweet
160 *a*	236		
161 *b*	182		
" *d*	196		
163 *a*	319		
163 *b*	194	4	
" *c*	267	1	
" *e*	74		
161 *c*	297	3	
161 *e*	202	2	
160 *c*	114	1	
160 *e*	173		
160 *i*	143		
	2,397	11	

From the two F_2 lots Nos. 165 and 166 of extracted sweet kernels which came from ear 130 *d* nine F_3 ears and nubbins were obtained (165 *a–d* and 166 *a–e*). The parent kernels and the ears obtained differ in aleurone color but as in the previous case of dents and flints, they may be considered as one series with reference to the characters sweet and starch. Of these nine ears seven

were relatively good sweets with only a small number (two to eight) of intermediate kernels while two (Nos. 166 *a*, *c*) showed a larger number of intermediates, one of them (166 *c*) showing also four kernels that I have classed as dimpled dents and thirteen kernels that I have classed as flints. This ear also showed six kernels in the special class of intermediates which are chimaera-like, with one half plump starchy and the other half wrinkled sugary in appearance. This is the highest number of such kernels that I have so far observed in a single ear. I have classed them with the intermediates in my general averages but their number is too small to appreciably affect the results.

TABLE II (*con.*)

C. Selected sweet kernels planted

c. Mixed ears, but prevailingly sweet (recessives)

Ear Nos.	Dimp. Dent	Flint	Intermediate	Sweet	Chimaera
166 *a*.......			61	255	
166 *b*.......			7	218	
166 *c*.......	4	13	56	70	6
166 *d*.......			3	337	
166 *e*.......			3	50	
165 *a*.......				225	
165 *b*.......			8	197	
165 *c*.......			2	117	
165 *d*.......				25	
	4	13	140	1,494	6

The classes and numbers of kernels for these nine ears (165 *a–d*, 166*a–e*) are given in TABLE II, section 1, *C*, *c*, and show when compared with the results given in TABLE II, section 1, *A*, that in this case the number of intermediate kernels found in ears from F_2 kernels selected as sweet is much smaller (about 8 per cent) than in ears from kernels selected as intermediate (about 40 per cent. In ears from starchy kernels there is only about 3 per cent of intermediate kernels (TABLE II, section 1, *D*).

We have clearly enough, it seems to me, in the offspring of this single F_2 ear (130 *d*) the picture of a case of fluctuating modification of characters by crossing with a further fluctuating tendency to inheritance of the modification suggesting the possibility of obtaining a fairly pure race intermediate, in respect to the characters considered, between the parent races.

The data furnished by the offspring from the further ears of the same F_2 generation (130 *a*, 129 *a*, *c*) suggest the same conclusion. These lots again were selected with reference to variations in aleurone color and for this reason further intermediates were not planted, but as before we shall consider at this time only the starchy and sweet characters.

TABLE II (*con.*)

D. Relative proportion of intermediate kernels obtained in F_3 from Wisconsin White Dent × Black Mexican by planting intermediate, as compared with starch and sugar kernels from ear 130 d

		From starchy kernels, 34 ears		From intermediate kernels, 7 ears	
		Typical	Interm.	Typical	Interm.
Extr. hybr. 12 ears	starchy	1,390		173	616
	sweet	369	154	748	
Extr. dom. 12 ears	starchy	2,397	11		
	sweet				
		4,156	165		
		From sugar kernels			
Extr. rec. 9 ears	starchy	17			
	sweet	1,494	146		
		1,511	146	921	616

From ear 130 *a*, I grew in 1914 plants from four types of kernels, Nos. 155–158, 155 from colored flint kernels, 156 from white flint kernels, 157 from colored sweet kernels, 158 from white sweet kernels. From the starchy kernels eighteen ears were obtained. Ten of these ears would be classed as hybrids and in addition to typical starchy and sweet kernels, gave a much higher proportion of intermediates than the eight ears which would be classed as extracted dominants. In the former, TABLE II, section 2, *A*, *a*, there is one intermediate to thirty-nine starchy and sweet, in the latter, TABLE II, section 2, *A*, *b*, only one intermediate to 138 starchy. If we divide the intermediate kernels from the ten hybrid ears from this parent equally between the starchy and sweet classes we get 1772.5 starchy to 524.5 sweet, a ratio per four of 3.084: .913.

From the extracted sweet kernels (Nos. 157 and 158) ten ears were obtained. Eight of them were quite true to type as sweets

but one (158 *b*) showed a high percentage of intermediates and one a considerable percentage that were not fully wrinkled (157 *d*).

TABLE II (*con.*)

2. EARS FROM SELFED F_2 EAR 130 *a*

A. Starchy kernels planted

a. Mixed (hybrid) ears

Ear Nos.	Starchy	Intermediate	Sweet
155 *a*.	82		15
" *g*.	116		39
" *j*.	242	7	78
" *h*.	240	5	55
" *l*.	207	17	45
156 *a*.	145	10	33
" *b*.	214	3	65
" *c*.	222	1	82
" *d*.	144	12	36
155 *e*–1	132	2	48
	1,744	57	496

b. Slightly mixed ears (extracted dominants)

Ear Nos.	Starchy	Intermediate	Sweet
155 *b*–1	96	1	
" *d*.	329	1	
" *f*.	240	10	
" *h*.	141		
" *i*.	434		
" *m*.	140		
156 *e*.	160		
" *f*.	118		
	1,658	12	

TABLE II, section 2, *B*, *c*, gives the composition of these ears in detail and shows that from kernels selected as typically of the wrinkled sweet type when selfed one in every thirteen of the offspring appeared as intermediates, or as less wrinkled than is characteristic. This is a higher proportion of intermediates than was obtained from the so-called hybrids from the same parent ear (130 *a*) which gave one intermediate to thirty-nine starchy and sweet, and a very much higher proportion than came from the corresponding extracted dominants which gave only one intermediate to 138 starchy. The five full starchy kernels in ear 158 *a* and the four similar kernels in ear 157 *i*, were possibly from stray pollen though several of the intermediate kernels on ear 158 *a* which were probably the result of selfing were very close to starchy types while showing undoubted wrinkling.

TABLE II (*con.*)

B. Sweet kernels planted

c. Slightly mixed ears (recessives)

Ear Nos.	Starchy	Intermediate	Sweet
158 *a*.	5	10	316
" *b*.		78	103
" *c*.		4	139
157 *c*.			386
" *d*.		32	171
" *e*.			249
" *f*.		23	105
" *g*.			325
" *h*.		11	128
" *i*.	4	2	242
	9	160	2,164

From ear 129 *a* of this same cross, Wisconsin White Dent × Black Mexican sweet, eight different lots of kernels (Nos. 168–175) were planted in 1914. Lots 168, 169, 170, and 175 were from kernels dimpled dent in type. Lots 171–174 were from sweet kernels. No. 173, which was a pale sweet kernel, failed to produce any ears.

From the dimpled dent kernels 168, 169, 170, and 175 I obtained twenty ears. Six ears consisted largely of pure starchy kernels with few intermediates. These would be classed as extracted dominants. The number of starchy kernels and the number of intermediate kernels for each of these ears is given in TABLE II, section 3, *A*, *a*. The proportion of intermediates to starchy kernels for the six ears is about 1:185.

Sixteen ears gave both starchy and sweet kernels and would be classed as hybrids. The number of starchy intermediate and sweet kernels for each of these ears is given in TABLE II, section 3, *A*, *b*. For the whole series of sixteen ears there is a proportion of one intermediate to ninety sweet and starchy taken together. If we divide the intermediates, putting half of them with the starchy and half with the sweet kernels, we have 1981.5 starchy to 660.5 sweet kernels an exact 3:1 ratio. Assuming that the differences in wrinkling and translucency are really negligible and that some of the intermediates really belong with each of the two starchy sweet classes, such results as these and the preceding have been generally regarded as evidence of so-called purity of stock, homozygosity.

TABLE II (*con.*)

3. EARS FROM SELFED F_3 EAR 129*a*

A. Starchy kernels planted

a. Slightly mixed ears (dominants)

Ear Nos.	Starchy	Intermediate	Sweet
168 *a*	146	2	
" *m*	149	1	
169 *a*	232	2	
" *d*	92		
170 *b*	202		
" *d*	99		
	920	5	

b. Mixed ears obtained (hybrids)

168 *b*	199	5	94
" *c*	79	3	26
" *d*	178	7	45
" *e*	94		27
169 *b*	188	1	40
" *c*	89		24
" *e*	73		12
170 *a*	208		64
" *c*	133		59
" *e*	184		52
" *f*	93		31
" *g*	59	1	16
" *h*	89		47
" *i*	85		27
175 *a*	160	10	60
" *b*	56	2	22
	1,967	29	646

B. Sweet kernels planted

c. Slightly mixed ears obtained

171 *b*			176
" *a*			218
" *c*		9	138
" *m*			191
172 *a*		3	171
" *b*			77
" *c*			29
172 *d*			51
174 *a*			84
" *c*	3		90
" *d*			91
" *b*			120
	3	12	1436

From the kernels of this F_2 ear (129 *a*) selected to represent the sweet type I obtained twelve ears, nine of which showed only sweet kernels. Two (171 *c* and 172 *a*) showed respectively nine and three intermediate kernels. One ear (174 *c*) showed three full starchy kernels which may have been due to stray pollen as there were no intermediates on this ear. The classes of kernels for each of these ears is given in TABLE II, section 3, *B*, *c*.

From ear 129 *c* of the same cross four lots were planted, two (Nos. 176 and 178) consisting of dimpled dent kernels and two (Nos. 177 and 179) consisting of sweet kernels.

TABLE II (*con.*)

4. EARS FROM SELFED F_3 EAR 129 *c*

A. Starchy kernels planted

a. Mixed ears obtained (hybrids)

Ear Nos.	Starchy	Intermediate	Sweet	Chimaera and pitted
176 *a*	84	7	38	
" *c*	118	11	32	
" *d*	152		49	
" *e*	137	3	34	
" *f*	96	13	8	
" *m*	130	4	55	
178 *a*	293		88	5
" *c*	172	18	27	1
" *d*	191	1	86	
" *e*	163	1	61	
" *f*	105	6	37	
	1,641	64	515	6

From the dimpled dent kernels, thirteen selfed ears were obtained, two with for the most part pure starchy kernels which would be classed as extracted dominants and twelve giving starchy, intermediate, and sweet kernels which would be classed as extracted hybrids. In TABLE II, section 4, *A*, *a*, the composition of the mixed ears (extracted hybrids) is shown. The six kernels which show pitting, or one half sweet and one half starch (chimaera kernels) are counted with the intermediates. If the intermediate kernels are divided equally between the starchy and sweet classes we have here again an almost perfect Mendelian ratio, 3.008 starchy: .990 sweet. There is one intermediate kernel to thirty starchy and sweet kernels, a larger proportion than is found in the starchy ears.

The composition of the two extracted dominant ears is shown in TABLE II, section 4, *A*, *b*. The proportion of intermediate to starchy kernels is about 1:50.

TABLE II (*con.*)

b. Slightly mixed ears obtained (dominants)

Ear Nos.	Starchy	Intermediate	Sweet
176 *b*.............	163	5	
178 *b*.............	243	3	
	406	8	

From the sweet kernels, Nos. 177 and 179, seven ears were obtained whose composition is shown in TABLE II, section 4, *B*, *c*. Four of these ears show only sweet kernels while the other three show from one to fourteen intermediate kernels, the ratio for the whole group being about one intermediate to fifty-seven sweet kernels.

TABLE II (*con.*)

B. Sweet kernels planted

c. Slightly mixed ears obtained

Ear Nos.	Starchy	Intermediate	Sweet
177 *a*.............		1	322
177 *b*.............			238
177 *d*.............			216
177 *e*.............			28
177 *f*.............			32
179 *a*.............		14	193
179 *b*.............		6	182
		21	1,211

In 1915 this Wisconsin White Dent and Black Mexican Sweet cross was grown only for endosperm color in the attempt to isolate a pure blue race, and no intermediates between sweet and starch were planted, as the starchy kernels show the color more easily, especially in variegated kernels.

The fourth generation of these intermediates from the cross of Black Mexican Sweet by Wisconsin White Dent was grown in 1916. In this year an out cross was made in order to test the behavior of the intermediate condition in combinations from different sources. A series of kernels from one of the above F_3

selfed ears was grown and the silks pollinated from another coffee-colored intermediate obtained by crossing two well-marked sweet races. The male parent of this intermediate was the Black Mexican Sweet used in the parentage of the series so far considered. The female parent was Ruby Sweet, a form obtained from Childs in 1913 and grown and selfed in that year. Kernels from one of these selfed ears were grown in 1914 and crossed with Black Mexican Sweet. The F_1 ears so obtained showed a mixture of sweets and intermediates and the intermediate kernels selected from one of these ears (74 *a*) were made the starting point for a series of intermediates which have been continued now through four inbred generations (1914–1918). These intermediates did not at once breed true. They showed varying proportions of sweets, intermediates, and fully smooth, flint-like kernels. Halstead ('07, '08, '09) has described a similar case of the origin of an intermediate Malamo from two sweet races, Malakan and Premo. He bred the type for a number of years with open pollination and by selection of sweet and flinty kernels obtained a marked increase in the starchiness and sweetness respectively of the ears.

His test plots showed ('08) that "ears from the plot planted with flinty kernels were largely flinty while the sweet grains gave ears that showed as a rule very little tendency to produce starch." He did not obtain, however, in either case types which would breed true. They probably showed a wider range of variability than was represented in the parents.

I shall describe this series more fully in the discussion of the use of these intermediates between starch and sugar types as special meal corns. Intermediate kernels from an ear of the F_1 (74 *a*) of this Ruby Sweet × Black Mexican cross were planted and used as the male parent for a series of other intermediate types, including those between Wisconsin White Dent and Black Mexican Sweet which we have been considering. The male and the mother plants were planted in alternate rows and the mother plants were simply detasseled and left to open pollination from the coffee colored intermediate.

Three lots of kernels from ear 164 *b* (Table III, section 1, *A*) were planted in the 1916 plot as the F_4 generation of the Wisconsin White Dent × Black Mexican Sweet series. No. 750 consisted of

dimpled dent kernels, No. 751 of intermediate kernels and No. 752 of sweet kernels. All these were grown and pollinated by the intermediate from Ruby Sweet × Black Mexican, No. 763, as male parent. The ears obtained in this way were all small as a result of the selfing in the F_2 and F_3. The kernels selected as dimpled dents, No. 750, failed to come so no results in this particular combination were obtained.

The intermediate kernels from this ear gave two ears, 751 *a* and *d*, with almost wholly intermediate and sweet kernels, two ears on one stalk, 751 *c* 1 and *c* 2 wholly flint in type, and one ear, 751 *b* which gave flint, intermediate, and sweet kernels. The classes are shown in TABLE III, section 1, *A*; 48+ per cent are starchy, 31+ per cent intermediate, and 20+ per cent sweet.

TABLE III. OUT CROSS IN 1916, F_3 OF RACE SELECTED AS INTERMEDIATES FROM WISCONSIN WHITE DENT BY BLACK MEXICAN SWEET × THE F_1 INTERMEDIATE FROM A CROSS BETWEEN TWO SWEET TYPES, RUBY SWEET × BLACK MEXICAN SWEET

1. EAR 164 *b* AS PARENT

A. Intermediate kernels planted

Ear Nos.	Flint	Intermediate	Sweet
751 *a*		186	77
751 *b*	114	67	67
751 *c*–1	78		
751 *c*–2	292		
751 *d*	3	61	57
	487	314	201

The distinction between sweet and intermediate in all these ears was very difficult in many kernels, though that there were the three classes present was obvious. The results are of interest as showing that in this out cross, though the new male parent came from two sweet parents, the capacity to produce kernels and even entire ears of the full starchy type has not disappeared in this intermediate series. The fully wrinkled sugar kernels are perhaps even more persistent though pure sweet ears were not obtained.

Three other nubbins, 754 *a–c*, from intermediate kernels of ear 164 *b*, were obtained from ears grown in the greenhouse but were too poorly developed to be considered.

The kernels selected as fully wrinkled, No. 752, from this F_3 ear (164 *b*) also gave a mixed result when pollinated by the Ruby Sweet × Black Mexican Intermediate. Four ears were obtained Nos. 752 *a* 1 and *a* 2 from the same stalk, 752 *b*, and 752 *c*. The classes of kernels are given in TABLE III, section 1, *B*. There are 42 per cent intermediate and 57 per cent sweet.

TABLE III (*con.*)

B. Fully wrinkled sweet kernels planted

Ear Nos.	Flint	Intermediate	Sweet
752 *a*–1		22	140
752 *a*–2		75	97
752 *b*		233	79
752 *c*		17	162
		347	478

The ears verge strongly toward pure intermediates in their general appearance but it is difficult if not impossible in the case of many kernels to decide whether they should be classed as sweet or intermediate. It seems quite unnecessary to figure these ears or the remaining ones of the series as the grades of wrinkling are similar to those shown in the figures given for the F_3 generation. A lot of intermediate kernels from ear 164 *c* showed the result of the selfing in the F_3 still more markedly. Fourteen small ears and nubbins were obtained all but two, 753 *c* and 753 *k*, were poorly filled. Ear 753 *c* was quite uniformly intermediate. Ear 753 *k* verged more toward sweet. The scattered kernels on the other ears and nubbins were hard to classify owing to the flattened and abnormal forms regularly found in such scattered kernels and I have not attempted to summarize the results of this planting.

A lot of intermediate kernels from the F_3 ear 164 *d*, sister to 164 *b* and 164 *c*, gave four ears, 754 *e–h*, with a large proportion of rather typically intermediate kernels. The classes are given in TABLE III, section 2. There are 55+ per cent intermediate, and 44+ per cent sweet. One ear, 754 *f*, showed more sweet than intermediate kernels. All four ears showed some kernels strongly verging toward flints in their appearance. These kernels are somewhat opaque and their wrinkling is very delicate, scarcely perceptible in some cases.

TABLE III (*con.*)

2. EAR 164 *d* AS PARENT (SEE TABLE II, SECTION 1, *A*)

A. Intermediate kernels planted

Ear Nos.	Flint	Intermediate	Sweet
754 *e*		65	53 Many flint-like
" *f*		102	146
" *g*		83	26 { Many flint-like but minutely
" *h*		153	92 { wrinkled kernels
		403	317

Ten small ears and nubbins, Nos. 758 *a–f* were obtained from the F_3 ear 164 *f*. The classes of kernels are given in TABLE III, section 3. There are a few scattering kernels in this lot which are plump and opaque and may be classed as starchy. The intermediates are for the most part quite typical. In the whole series there is a preponderance of sweet kernels but many kernels classed as sweets verge strongly toward intermediates. The ratios are .2+ per cent starchy: 46+ per cent intermediate: 53+ per cent sweet.

TABLE III (*con.*)

3. EAR 164 *f* AS PARENT

Intermediate kernels planted

Ear Nos.	Starchy	Intermediate	Sweet
758 *a*–1		127	54
" *a*–2		100	24
" *b*–1	1	106	48
" *b*–2		72	68
" *c*–1		44	69
" *c*–2		15	31
" *c*–3	1	82	84
" *d*	2	22	160
" *e*		20	180
" *f*		78	68
	4	666	786

Four small ears, Nos. 759 *a–d* were obtained from intermediate kernels from ear 166 *a*. The classes from these ears are given in TABLE III, section 4.

One ear, 759 *a*, is almost wholly sweet in type. The other three are markedly intermediate in general appearance, but many of the kernels are very hard to classify. The proportions are 55+ per cent intermediates and 44+ per cent sweet.

Considering this whole F_4 out cross generation, we find that when intermediate kernels were planted they predominate slightly over the sweet. The proportions are from intermediates: starchy 12+ per cent, intermediate 46+ per cent, sweet 41+ per cent. The appearance of the large number of flint kernels in the progeny of the intermediate kernels from ear 164 *b* is notable as showing

TABLE III (*con.*)

4. EAR 166 *a* AS PARENT

Intermediate kernels planted

Ear Nos.	Starchy	Intermediate	Sweet
759 *a*		4	259
" *b*		119	72
" *c*		198	22
" *d*		161	34
		482	387

the persistence of the capacity to return to a fully starchy type, especially since as noted the new male parent came as a cross from the two sweet races Ruby Sweet and Black Mexican Sweet. The sweet kernels planted from this same ear also gave a preponderance of sweet, 57+ per cent sweet to 42+ per cent intermediate.

GENERAL DISCUSSION

1. SIGNIFICANCE OF THE INTERMEDIATES

From these four generations of a cross between a sweet and a dent corn, the evidence is very clear, it seems to me, that what can be interpreted as a separation of the parental germ plasms in the reduction divisions and recombinations of the gametes so produced according to the laws of chance actually occurs as East and Correns found and as has been shown cytologically and assumed generally in Mendelian conceptions. It is, however, equally plain that provision must be made in such theoretic conceptions for the occurrence of intermediates. There is evidence of segregation (chromosome reduction) but not of the so-called purity of the gametes. We might assume here in accord with current practice factors acting as modifiers, inhibitors, etc., with varying efficiencies in the case of different kernels, but there is no adequate

evidence that any such assumed factors are distributed in the reduction divisions in any clear-cut and obvious fashion, such as the simple mono-hybrid ratios, and to name in the germ plasm the same qualities observed in the soma explains nothing and is merely the old preformationism in a modern guise.

Correns ('01) and East and Hayes ('11) have based their generalization that the qualities starchy and sugary make a typical Mendelian pair of characters in their segregation and recombination behavior on the assumption that intermediates behave, when grown and selfed, practically like the visibly more typical starchy or sweet kernels, except in rare cases of mutation, when as East reports an occasional intermediate ear (1 in 10,000) appears with no evidence that it is a result of hybridization and whose offspring tend to breed true, thus causing trouble to growers of sweet corn for canneries in case such ears are not avoided as seed.

That however both in their behavior in the following generation and in their appearance there is adequate ground for treating the intermediates as a special class is, it seems to me, sufficiently evident from the data given above. In TABLE II, section *1*, *D*, I have brought together and compared the results obtained by planting intermediates with those obtained by planting typical starchy and sugary kernels from ear 130 *d*. About 40 per cent of intermediates were obtained from planting intermediates, while ears from sweet and starchy kernels gave only about 5 per cent of intermediate kernels. The evidence from Correns's work as well as my own is overwhelming that such intermediate kernels do occur sporadically but quite commonly as a result of crossing as well as congenitally as a result of sexual reproduction in so-called pure races and that in whatever way they arise, they do not at once breed true. By selection the percentage of such kernels may be increased with fair probability in every case that rather pure races of intermediates may be established. Selection of intermediates through the F_2 and F_3 generations selfed followed by an out cross with an intermediate of different parentage gave as the progeny of one ear (166 *a*) three out of four ears with a considerable excess of intermediates and with no pure starchy kernels. The fourth ear was an almost pure sweet. The off-

spring of the other F_3 ears gave more mixed results. Since but one generation can be grown in a year, it is a slow process to test out the effects of selection, particularly in view of the bad effects of inbreeding, but it seems to me the results given are conclusive for this particular case at least, though the particular point with which I am concerned is to show that sporadically occurring intermediates arising in crossed ears do not behave when grown and selfed like ordinary sweet or starchy kernels, but show that the intermediate condition is also heritable in a very considerable degree.

There is evidence also that in the whole F_2 and F_3 of this cross of Wisconsin White Dent by Black Mexican Sweet, we not only obtain more intermediate kernels by planting intermediates than are obtained by planting sugary or starchy kernels of the same ancestry, (see p. 159) but also intermediates are relatively more numerous in the offspring of the so-called extracted recessives and of the mixed starchy and sweet ears (about 3 per cent) than in the offspring of the kernels that gave so-called extracted dominants (only .6 per cent). In the so-called extracted recessive ears of the F_3 taken by themselves there are about 5 per cent of intermediate kernels. Selected intermediate kernels give a higher percentage of intermediates, but intermediates occur in not inconsiderable numbers in both so-called pure extracted dominants and extracted hybrids, more in the latter than in the former. It would seem that the sweet character is in less stable equilibrium, so to speak, than the starchy character and that sweet types are more likely to vary toward starchy than are starchy types toward sweet types. The intermediates are not merely chance variants diverging with equal frequency from both starchy and sugary types. This is a tendency of the same order perhaps as that which has been observed by Collins and Kempton, who find as noted an excess of starchy over waxy kernels in their crosses of these types.

It is generally recognized that the starchy kernel is the more primitive type of corn and that the sweet races have been derived from the starchy races, though the whole process is prehistoric and there are no positive records, so far as I am aware, of the origin of a sweet race from a starchy race where the possibility of crossing

was excluded. To obtain a starchy race from a sweet race is much easier. I have practically pure flint ears, as far as appearances go, from the above described cross of Ruby Sweet and Black Mexican.

It is worthy of note here that from this dent sweet corn cross quite a percentage of flint kernels appear. East has also noted this fact in a similar case and regards it as showing that Black Mexican Sweet had a flint corn in its ancestry and carries latent flint. He believes that the sweet corns are of two groups in this respect, derived respectively from dent and flint ancestries and that their behavior in crosses with dents and flints will indicate to which of the classes they belong. In view of the fluctuating character of both sweet and starchy characters in crosses such a contention is difficult to test. As bearing on the whole question as to the significance in practical breeding work of the occurrence of fluctuating variants between the parental types in crossing it is worth while to quote here the final paragraph of a recent paper by Kempton ('19), based on his own and Collins's work on the inheritance of endosperm characters in corn.

> For the breeder of crop plants where most of the desired characters are almost infinitely complex, seldom alternative, and often intangible, Mendelism seems to have little of practical value to offer, whether the attempt of some investigators to so extend the theory as to embrace such characters be approved or not. While Mendelism may assist in making desired combinations, there is nothing to show that it can serve as a substitute for selection either in finding the best stocks or in preserving them from subsequent deterioration.

Collins and Kempton have perhaps done more than any others to broaden our knowledge of the behavior of corn in crossing, and the above statement is particularly interesting in view of the sweeping generalizations found in such a book as that of Babcock and Claussen.

2. Pairing of parental chromosomes, reduction divisions, and segregation

The occurrence of intermediates need not as noted lead us to question the cytological evidence for the segregation of the chromosomes from the male and female parents respectively in the reduction division and the chance recombination of these chromosomes in the succeeding fertilizations. The cytological

evidence for pairing of the homologous chromosomes from the two parents as indicated by length and other differential characters is accumulating rapidly both for plants and animals. For data as to plant material see Strasburger ('05), Stomps ('10) and Clemens Müller ('09 and '12).

While we need more convincing proof of the relationship of the processes in the so-called first and second divisions to the process of the reduction of the chromosome number there can be no question now that in general the sporophyte is a double or combination individual and that the chromosomes contributed by its two parents maintain a sort of individuality even when so combined.

Cytological evidence is as yet quite lacking as to just when and how in fertilization or in the succeeding divisions the homologous chromosomes are able to find each other out and attain the paired relationships which the sporophytic division figures show so clearly. Sax ('18) reports for *Fritillaria* and *Triticum* that they do not pair in the first division of the fertilized egg. Resort to conceptions of chemical affinity, magnetic polarities, etc., are of course useless here and our best suggestions, as it seems to me, are found in the conception of permanent connections or space relations between chromosomes and the mechanically active kinoplasmic elements of the colloidal cell organization which are indicated in Rabl's figure ('89), the constant relations between centrosome and nucleus observed by Conklin in *Crepidula* ('02) and the visibly permanent connections found between central bodies and chromosomes in the ascus ('97).

The pairing of the germ cells with each new fertilization is determined by the external environment and is a matter of chance, but the homologous chromosomes of each probably become paired through the mechanical activities made possible by the cell organization constituting the internal environment of the cell elements. We arrive here at a more precise conception of what may constitute the internal environment of the germ plasm than has hitherto been possible, though the assumption of an effective internal environment has seemed necessary to many on other grounds as well.

However the pairing may be brought about, there is general agreement that it has been achieved completely at synapsis and

for plants at least the visible appearance of the synaptic knot and the succeeding pachyneme spireme suggest that at this stage the chromosome pairs may become very intimately combined (Allen '05). On *a priori* grounds it would seem unlikely that such complex and labile compounds as we may suppose constitute the germ plasms should enter into such close physical relations of fusion without a greater or less amount of mixing and interaction which would more or less permanently alter their character. That the degree of such interaction should be the same in every case even of the same cross would seem to be quite improbable. It would be natural enough that many grades of interaction might occur in the synaptic stages leading to the formation of the eggs on a single ear of corn or the pollen grains of a single anther sac. The possible variability suggested by the cytological data as to synapsis forms a natural parallel to the variable degrees of mixing of the sugar and starch characters shown in the F_2 hybrid ears, resulting from the pairing of gametes from sugar and starch corns in the F_1.

3. Relation of sexual reproduction to variation

If corn endosperms could be reproduced vegetatively such intergradations as we are discussing would doubtless occur as bud variations, like those Stout has described for *Coleus* ('15), but it is of importance to note that here they regularly follow sexual reproduction and it seems to me are to be regarded as the natural expression of the likelihood that processes so complex as we now know those of sexual reproduction are, should result in a higher percentage of variants than results from purely vegetative reproduction involving in the last analysis only nuclear and cell division. We need perhaps further careful statistical studies like those of Stout on species like *Coleus*, which can be propagated in both fashions to determine the relative frequency and degree of bud variation as compared with variation in sexually reproduced progeny. As it is we have the experience of commercial growers that in many cases in which seed progenies are quite variable progeny produced vegetatively by cuttings, etc., are sufficiently constant to be a reliable means of introducing and propagating important types of fruits and vegetables. No one questions that it is in general regarded as much easier to establish and fix a new variety which

can be propagated vegetatively than one which can only be propagated by seed. It seems to me that the evidence suggests that the general occurrence of intermediates as a result of crossing is due not only to the bringing together of divergent or contrasting pairs of characteristics but to the exigencies of sexual reproduction itself. It is easy to say that the combination of two equivalent things cannot result in variation but aside from the question as to whether male and female gametes ever are equivalents in any very strict sense it seems also obvious that the pairing of such complex colloidal systems as are the germ cells constitutes for each of the two individually as well as for the diploid unit which is coming into being an especially critical stage whose end result may very well show considerable fluctuating variability and in turn result in fluctuating congenital variability in the progeny.

An ear of corn with its large numbers of easily preserved and studied individual examples of such fusions produced under conditions involving a minimum of environmental variation is very favorable material for the recognition of such fluctuations. To be sure ears of pure bred races may show striking uniformity in their kernels especially in the starchy races but in the sugar corns variations in the degree of wrinkling are as I have found by no means rare occurrences. We must recognize without doubt as has long been obvious to the systematists fluctuating variability in the character of species as to their tendency to constancy or variability in their seed progeny. Some species or races show a high degree of fixity of type while others are just as truly characterized by their variability. There is nothing inconsistent with such facts in what we know of the relative fixity of the physical characteristics of various substances in the colloidal condition and of colloidal systems made up of varying proportions of the different elements or of different colloids.

What is true however of the chances of fluctuating variability in the offspring of gametes from individuals of the same so-called pure race is doubly true in the case of crosses between races differing in one or more characters. That the pairing of germ plasms from congenitally different parents should regularly and in every species result merely in a shuffling of fixed unit factors is out of harmony with what we know of the ordinary behavior of such viscid

colloidal aggregates as the gametes and the chromosomes when brought into such intricate relations as are the elements of the homologous pairs of chromosomes in the synaptic knot and the subsequent pachyneme spireme. Speaking in terms of chemistry and molecules no chemist would expect to be able always to isolate in a pure state by physical means alone such complex and unstable compounds as the proteins after they have been so intimately combined.

It seems to me necessary here to keep in mind always in connection with our theories of heredity and the structure of the germ plasm the known facts as to such polyphase colloidal systems as the cells appear to be. That the homologous chromosomes do pair, combine in the synaptic knot, separate in the reduction divisions, live a longer or shorter independent existence in the gametophytic generations, and then become paired again sooner or later as a result of gametic fusion are facts established from cytological observations and confirmed in their broad outlines by the evidence from breeding experiments for segregation and chance recombinations of characters. That however the germ plasms remain unaltered through these reproductive processes is not shown by breeding results and is quite inconsistent with what we should expect to be the results of the observed cytological processes on the viscid colloidal materials of the gametes as wholes and on the chromosomes themselves.

As noted corn with its large number of individual endosperms showing characters easily studied which can be obtained simultaneously and in parts of the ear under practically identical environmental conditions though each is the product of a distinct, free, and chance-determined pollination (in selfing so far as the variations in pollen of the same individual is concerned, in open pollination so far as variation of pollen occurs in the whole field) affords very special advantages for the study of variation both within a race and in hybrids.

The difficulty in distinguishing between variations which are due to environment and those which are germinal and congenital largely disappears in the case of these endosperm characters. Aside from the peculiar and apparently epigenetic cases of the pitted and chimaera-like kernels, it is easy to distinguish the

relative effects of environment and heredity on the form of the kernels and the degree of the wrinkling. Kernels at the butt of the ear tend to be smoother as a result of extreme pressure from the husks in this region. The kernels at the tip also show the effects of exposure if the husks are too short or of pressure if the husks are long and heavy, so that a well filled ear in its longitudinal growth meets considerable resistance from them. The hundreds of kernels in the middle region of the ear relatively to each other have a remarkably constant set of conditions through the whole of their development and the variations in their form are very obviously from their chance distribution to be interpreted as the expression of the exigencies of the fusion and pairing processes of fertilization, plus the particular and general qualities of the gametes which fuse and the chromosomes which pair. It has been too commonly assumed that the variations in the progeny of a pure race or the progeny from the crossing of two pure races must be largely if not wholly due to the external environment. With our increased knowledge of the complicated processes which are involved in synapsis, the reduction divisions, gametic cell fusions and the final pairing of homologous chromosomes it is obvious that at each and all of these stages there are abundant opportunities for variations in the germ plasm arising both from the chemical and physical interactions of the complex and labile materials of the chromosomes upon each other and of the cytoplasm, spindle fibers, etc., upon the chromosomes. As a single illustration take the frequently observed and figured cases of the occasional chromosome pairs which for one reason or another remain for some time connected in the equatorial plate and are tremendously elongated and distorted in being pulled back to the poles. In any theory of their nature and structure there is at least a chance that such a pair have been modified in some way and are different than their neighbors either before or as a result of this special variation from the normal processes of chromosome separation. Their position in the daughter group of chromosomes is for a time at least visibly modified. With the discovery of the normal paired relation of the homologous chromosomes of diploid nuclei the whole matter of the space relations of the chromosomes with reference to each other, to the centrosome and

to the nuclear membrane is coming to be recognized as a problem of fundamental cytological importance. These interrelations of the cell structures constitute as I have pointed out a sort of internal environment for the germ plasm but an environment from which in my opinion it is inseparable and which determines continuously in a considerable degree its constitution. With the recognition that all protoplasmic cell structures are phases of a complex of colloidal systems the question as to whether all change must not of necessity originate in environmental influence largely loses its point. That the position of the chromosomes with reference to the plasma membrane may be of significance, has been already claimed by Swingle in his theory of zygotaxis ('11, '13). That such conceptions seem far less fanciful, as our evidence for the individuality of the chromosomes and the reality of their paired positions in the diploid cells becomes more positive, cannot be questioned. During the period of the maturation and fertilization processes the germ plasm is best protected from, because it is least dependent on, the general external environment and in view of the complexity of these processes the claim that all change must be initiated by influences from outside the organism can have little weight. Changes resulting from the functioning of the mechanism of chromosome pairing and reduction, and gametic fusions may well be characterized as due to the normal capacity of the germ plasm for congenital variation. I am not suggesting here any doctrine of spontaneous or self-caused change, but am only pointing out that the stages of embryo initiation, from their obscurity and our ignorance of them, have been either regarded as of no significance (Lamarckian emphasis on influence of external environment) or have been given an exaggerated and strictly theoretically conceived importance (doctrines of germinal variation) in initiating variation and even evolutionary advance. With our better knowledge, we now see, from the very complexity of the mechanisms concerned and the fundamentally new relations into which the gametic cells enter in the act of fusion, there may well result at least what we may perhaps properly call with Meehan and Cook ('19) the normal fluctuating variation of the organism.

We realize more fully now than Darwin did that the question as to whether sexual reproduction is in itself a source of variation

or a means of swamping out existing variations involves the consideration of the complicated and far reaching mechanical and chemical interrelations of the cell structures concerned in the preparation for, and achievement of, cell or gametic fusion and the pairing of the chromosomes. It is obvious that we must distinguish at least two somewhat independent sets of conditions which determine the character of the embryonic progeny in sexual reproduction. First, the degree of similarity or difference in the ancestry of the gametes which are to combine and, second, the very processes of synapsis, maturation and union of the gametes. To be sure each of these sets of conditions determines the other in large degree. First, the complicated nature of the processes of reproduction set a limit to the degree of difference allowable in the gametes beyond which even if fertilization occurs embryo abortion may at once follow. Second, owing to the complexity of the fertilization process the degree of compatibility in the gametes may influence the probable range of variation in the progeny as well as their general vegetative vigor and fertility or sterility when grown.

It seems to me probable that the constitutional differences in the gametes are more likely to be responsible for the wider and so-called suddenly achieved variations known as mutations, sports, monstrosities, etc., while the complex nature of the reduction, mating, fusion, and pairing prcesses may well be regarded as responsible for those fluctuating normal variations which it has been so much the fashion recently to confuse with the not directly heritable variations due to the external environment.

It is not at all impossible of course that external environmental conditions of temperature, and nutrition, toxic effects, etc., may influence the complex of reproductive processes and thus affect the degree of congenital variation. The demonstration of this, however, by such studies as those of alcoholism, malnūtrition, etc., in their influence on the offspring of sexual reproduction have so far led to no very conclusive results.

It is clear then, it seems to me, that the cytological discoveries as to the nature of synapsis, chromosome reduction, gametic fusion and chromosome pairing indicate that fluctuating variation may be expected as a direct result of the complexity of these

processes. The congenital characteristics of a series of hybrid offspring from the same pure bred parents and produced at the same time are not to be expected to be identical. Offspring from inbreeding or from selfing in a so-called pure race may also show congenital fluctuating variations due to the inherent nature of the sexual processes and quite independent of the so-called racial purity of the parents as fixed by carefully controlled inbreeding.

The endosperm characters of corn are as noted especially favorable for the detection of such phenomena since we have here in the hundreds of kernels from the middle region of a good-sized selfed or inbred ear a series of offspring from independent matings developed to maturity under practically identical environmental conditions except perhaps for a slight progressive diminution in food and water supply as we proceed from the butt of the ear to its tip and a little more crowding due to the narrowing of the ear in some races. The effect of these factors on endosperm characters is apparently so slight as to be negligible. Variations between the kernels under these conditions are to be characterized from their time of origin as congenital and are to be expected to be more or less fully heritable as my results from selecting and selfing intermediate kernels between the sugar and starch characters show that they are.

It is easy to assign differences between flowers or leaves on the same plant or between peas or beans from different pods or from the ends of the pods as compared with their middle region to the effects of environment, but differences between peas or beans from the middle region of the same well-developed pod or between kernels from the middle region of a large, well-filled ear of corn must be congenital. In the corn especially it is possible to obtain numbers large enough from the same ear to study such variations statistically as I have done and arrive at the certainty of their fluctuating and none the less more or less fully heritable value.

A further advantage afforded by corn for the study of these fluctuating variations is found in the practical fact that these endosperm characters are permanent and the ears are easily stored and preserved for comparison with the new data obtained in each succeeding year. No other material I know of is so favorable in all these respects for the careful and quantitative study of the inheritance of variations.

In emphasizing the fluctuating variability shown in the inheritance of these endosperm characters it is not to be forgotten that commonly there are some F_2 kernels and some ears in which segregation is quite pure. By selecting these apparently Mendelian results may be secured, but it is just as true that there are always other kernels in which more or less mixture of the characters for sugar and starch has occurred, and by selecting these intermediates in larger proportions may be secured, and probably by continued selection pure races of intermediates can be produced. The possibility of the existence of equilibrium types is to be recognized, representing phases of greater stability in the germ plasm toward which fluctuations tend to converge. Breeders who in general terms report the confirmation of East's and Correns's results in corn have probably more or less consciously selected from the typical parental types in planting for the F_3 and succeeding generations.

4. Nature of the sugar and starch characters

The characters sweet and starchy are typically metidentical characters. The presence of sugars and dextrin gums in solution or in sols leads in drying out to shrinkage of the cell and an irregular outline just as the whole kernel becomes wrinkled and shrivelled. The presence of more solid starch grains packing the cells full prevents this shrivelling with loss of water and the cells and kernels remain plump and rounded. This is a case of a metidentical character expressing itself morphogenetically and giving characteristic form differences in a many-celled structure. So far as I know it is the only case of this sort so far noted, most metidentical characters being matters of color, taste, etc., and such properties as length of life, fertility, sterility, etc. The character starchy or sugary can be transmitted directly as such through the egg and male cell. There is no question here as to a method of its representation in the germ plasm. It need not be considered as represented in the germ cells by a factor or factors which are not fundamentally the same as the character itself in its expression in other cells. In a sugar corn, speaking broadly and so far as we now know, the endosperm cells tend to contain certain more soluble carbohydrates as storage products. In a starchy corn the endo-

sperm shows a tendency to produce starch in greater proportions as a reserve carbohydrate throughout the life of the endosperm cells. Such tendencies or qualities need not be conceived as represented but as actually present as such in the germ cells, and as coming to expression in varying degrees according to the position of the cell in the multicellular plant body and its corresponding opportunity for the formation of storage products. We of course need much further data, both histological and cytological as to the sweet and starchy kernels but no facts so far known are, as it seems to me, inconsistent with the conception of these characters as metidentical form qualities which can be classed with the metidentical color characters which are so common. That such form characters must be conceived as the expression of a definite number of unit factors invariable except for relatively rare and strongly marked mutations, seems to me quite contrary to the evidence as it exists. The fluctuating behavior of these characters with the presence of all possible intergradation from the extreme of starchy to the extreme of sweet, as shown in FIGS. 167 *b*–167 *f*, suggests modification and fluctuating variability rather than mathematical fixity in the cellular basis of these characters. The fact that selection does not, at least at once, eliminate the extremes of the series of variants is opposed to the conception of such variability being due to recombination of multiple fixed factors. Typically starchy kernels and typically sweet kernels recur in the F_3 and F_4 generations, as is shown in the tables. The number of generations is small, but the case is one again in which the relative proportion of the varying types is changed by selection without the immediate elimination or the obviously proportionate elimination of variability. This series was not continued further, as other intermediate types seemed more promising for productiveness and other matters of interest. As noted above, further data will be given in connection with the description of such intermediates as a possible race of meal corns. All of the starch × sugar crosses which I have studied show in general a similar fluctuating variability, with a tendency to the inheritance of the intermediate condition when it appears. The intermediates obtained in the Wisconsin White Dent × Black Mexican Sweet cross may be taken as illustrative, so far as my

observations go, of the general behavior of the sugar and starch characters when crossed. The data as to small fluctuating but heritable variations as given by Jennings ('16), Stout ('15), Hegner ('19) and others, for asexual reproduction in pedigreed cultures has shown that the long recognized fixity of type resulting from asexual reproduction while sufficient in many cases to enable the horticulturist and practical breeder to furnish a fairly stable product for the market, is by no means absolute. Much more is it true as shown by Castle and Phillips ('14) for rats, Stout and Boas for flower number in chicory ('18), as well as in much of the older literature of the subject, that in sexual reproduction, we are concerned not with fixed unit factors subject only to relatively rare mutations, but with fluctuating variability probably increased by the special vicissitudes of cell and nuclear fusion and chromosome pairing and reduction. Certainly the current interpretation, except for Jones's paper, of the behavior of the sugar and starch characters in corn as due to a pair of fixed Mendelizing factors, subject to only rare and relatively unimportant mutations, has not been in accordance with the facts, even as they were shown by Correns's great paper.

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Description of plates 3–5

Photographs and reproductions life size. Cards attached to the ends of the ears for pedigrees, data as to pollination, etc.

PLATE 3

FIG. 164 *a*. Kernels nearly all fully wrinkled and typical for sugar corn.

FIG. 164 *b*. Kernels showing many degrees of wrinkling but many of them tending toward translucency even when not fully wrinkled.

PLATE 4

FIG. 164 *c*. Kernels showing many degrees of wrinkling. The ear shows more opaque whiteness than 164 *b*.

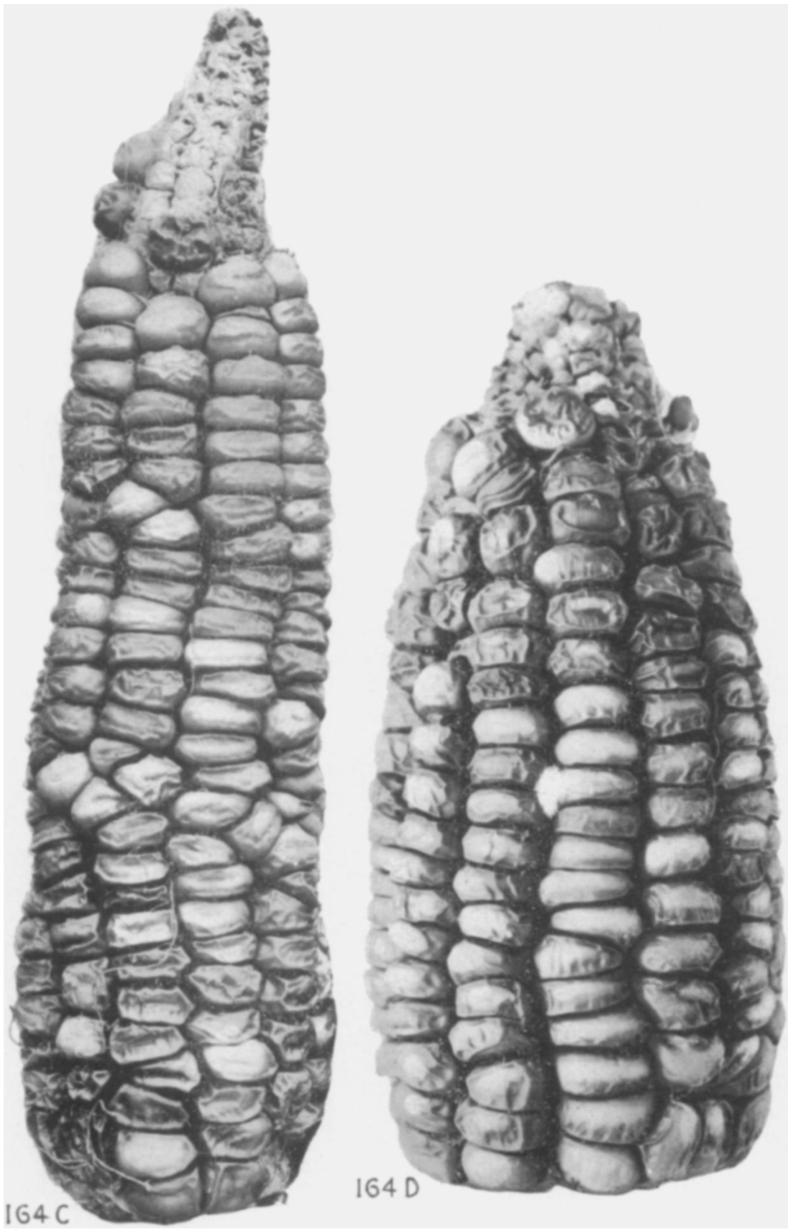
FIG. 164 *d*. The ear though short has more of the appearance of the dent parent. Many kernels however are fully wrinkled and translucent.

PLATE 5

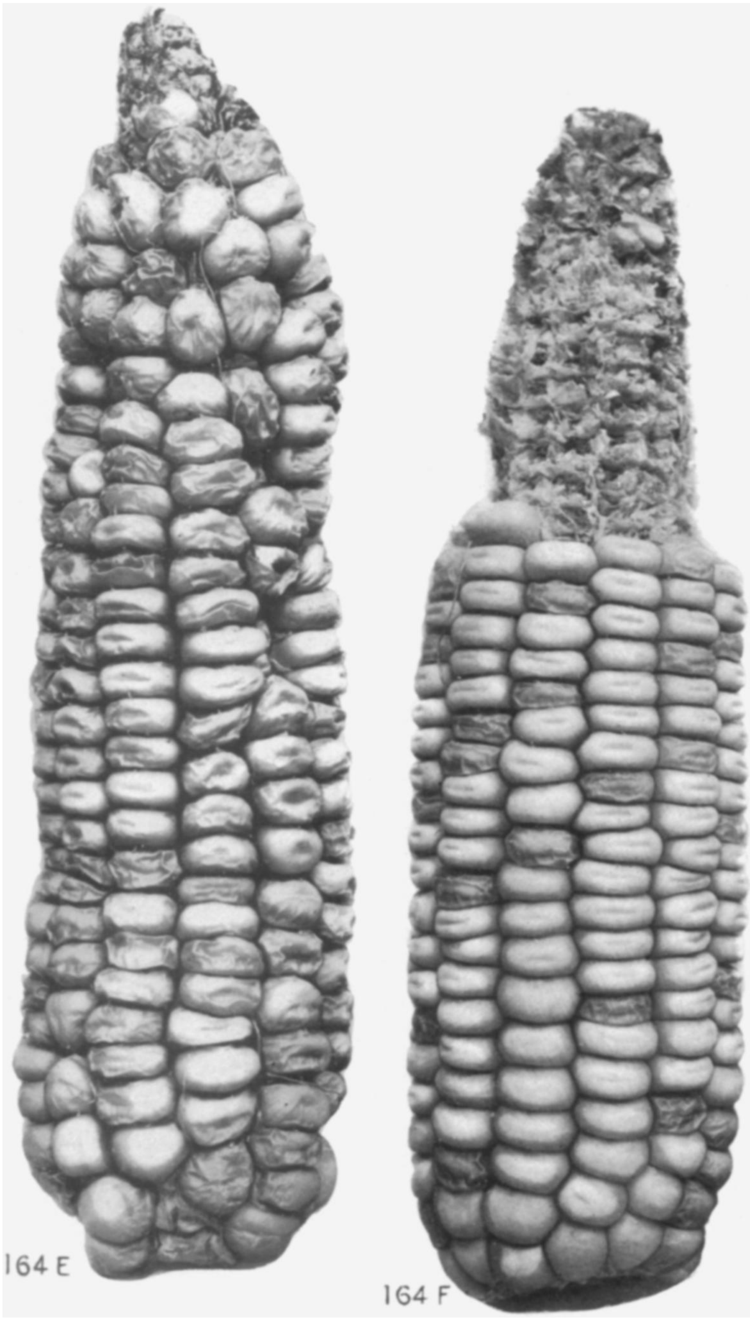
FIG. 164 *e*. The kernels are coarser and with much opaque white. Many of them quite of the dent type. Others are quite fully wrinkled.

FIG. 164 *f*. The ear was partly shelled by birds. It shows plump flint-like kernels, dimpled dent kernels, and fully wrinkled translucent sugary type kernels, as well as intermediates.

HARPER: INHERITANCE IN CORN



HARPER: INHERITANCE IN CORN



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